Brazilian Journal of Biology
ISSN 1519-6984 (Print)
ISSN 1678-4375 (Online)

http://dx.doi.org/10.1590/1519-6984.170424
Original Article

Spatial and temporal variations in fish assemblage: testing the zonation concept in small reservoirs

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Received: October 10, 2016 – Accepted: April 11, 2017 – Distributed: October 31, 2018
(With 12 figures)

Abstract

Large reservoirs usually present spatial gradients in fish assemblage, distinguishing three strata (littoral, pelagic, and bathypelagic) along the vertical and horizontal axes, and three zones (fluvial, transitional, and lacustrine) along the longitudinal axis. The main objective of this study was to assess if small reservoirs also present the spatial gradients in fish assemblage attributes and structure as already observed in large reservoirs. Fish surveys were conducted quarterly, from 2003 to 2008, in the Mourão Reservoir (Mourão River, Paraná, Brazil), using gillnets with different mesh sizes, arranged in all strata of all three zones. Community attributes (species richness and evenness) were calculated for each sample, and differences were tested using three-way ANOVA (factors: zone, strata, year). Community composition was summarized using Correspondence Analysis (CA) and differences were tested with three-way ANOVA for each axis, controlling the same three factors. Because of the high variability in reservoir water level through time, all analyses were made considering temporal variations. Species richness presented a decreasing trend from fluvial to lacustrine zones, and higher values in littoral strata, possibly because upper reaches and littoral regions provide better conditions for fish to feed and to reproduce. Evenness was considerably low, presenting high variability, and no evident pattern. The expected longitudinal gradient was not found in this study indicating longitudinal similarity, contrary to observed in large reservoirs. Vertical and horizontal gradients were observed in all sampling stations, indicating that abiotic and biotic conditions are influencing fish distributions within the reservoir.

Keywords: dam, longitudinal gradients, impoundment, gradient.

Variações espaciais e temporais na assembleia de peixes: testando o conceito de zonação em pequenos reservatórios

Resumo

Grandes reservatórios, em geral, apresentam gradientes espaciais da assembleia de peixes, distinguindo três estratos (litoral, pelágico e batipelágico) ao longo dos eixos vertical e horizontal, e três zonas (fluvial, transição e lacustre) ao longo do eixo longitudinal. O principal objetivo deste estudo foi avaliar se pequenos reservatórios também apresentam tais gradientes espaciais, nos atributos e na estrutura da assembleia de peixes, como já observado em grandes reservatórios. As coletas dos peixes foram realizadas trimestralmente, de 2003 a 2008, no reservatório de Mourão (Rio Mourão, Paraná, Brasil), com redes de espera com diferentes tamanhos de malha, dispostas em todos os estratos de todas as três zonas. Atributos da assembleia (riqueza de espécies e equitabilidade) foram calculados para cada amostra, e as diferenças foram testadas utilizando ANOVA tri-fatorial (fatores: zona, estratos, anos). A estrutura da assembleia foi sumarizada usando uma Análise de Correspondência (CA) e as diferenças foram testadas com ANOVA tri-fatorial para cada eixo, controlando os mesmos três fatores. Devido à alta variabilidade no nível da água do reservatório ao longo do tempo, todas as análises foram feitas considerando as variações temporais. A riqueza de espécies apresentou tendência decrescente, da zona fluvial até a lacustre, com valores maiores no estrato litoral, possivelmente porque locais à montante e regiões litorâneas proporcionam melhores condições de alimentação e reprodução para os peixes. A equitabilidade foi consideravelmente baixa, apresentando alta variabilidade e nenhum padrão evidente. O gradiente longitudinal esperado não foi encontrado neste estudo, indicando similaridade longitudinal, ao contrário do observado em grandes reservatórios. Gradientes verticais e horizontais foram observadas em todas as áreas amostradas, sugerindo que as condições bióticas e abióticas estão influenciando a distribuição dos peixes ao longo do reservatório.

Palavras-chave: barragem, gradientes longitudinais, barramento, gradiente.

1. Introduction

To identify the spatial distribution patterns of fish assemblages and the factors that drive these interactions is one of the greatest challenges for aquatic ecologists, especially in modified environments, such as reservoirs (Miranda and Raborn, 2000). The construction of dams, caused by the increasing demand of energy over the last decades (Tolmasquim, 2012), modified the natural structure and composition of fish fauna, and, consequently, species interactions (Gomes and Miranda, 2001), making it difficult to predict the organization of fish assemblages in a variety of environments (Agostinho et al., 2016).

Reservoirs are intermediate environments between rivers and lakes. In some cases, they are referred to as hybrid systems, with complex interactions, and therefore, more variable patterns (Kimmel et al., 1990). Moreover, the hydrological conditions vary widely, depending on how the dam is operated (Nogueira et al., 2012). These variations in characteristics as water level, flow velocity, and residence time may dramatically alter the fish assemblage dynamics over the spatial scale, varying from longitudinal (as in rivers) to vertical (as in lakes), and reverse (Noble, 1980; Agostinho et al., 2008).

Reservoirs tend to exhibit the pattern proposed by Thornton et al. (1990), on the longitudinal axis, which describes three distinct zones along the reservoir: fluvial, transitional, and lacustrine. These zones constitute a spatial upstream-downstream gradient with differences in flow velocity, sedimentation rate, nutrient concentration and water transparency. Additionally, these features are influenced by hydrological seasonality and dam operation procedures. Therefore, it is already evidenced that changes in each feature directly influences the structure of fish assemblages, and this may vary across time, depending on dam operation and water level (Thornton et al., 1990; Vasek et al., 2004; Agostinho et al., 2007a), including fishing (Okada et al., 2005).

On the horizontal and vertical axes, we can identify the littoral, pelagic, and bathypelagic strata (as in lakes). The littoral strata are more similar to natural rivers, and fish tend to inhabit these areas more frequently and efficiently (Agostinho et al., 2007b; Gido et al., 2009). The littoral also may exhibit high structural complexity (habitat heterogeneity) and greater amounts of organic matter, due to the decomposition resulting from water level variations, and also because some species of fish uses them as nesting areas (Fernando and Holcik, 1991; Baumgartner et al., 2008). On the vertical axis, riverine fish rarely inhabit the pelagic and bathypelagic strata. The reasons for the low abundance in the pelagic are mainly the low productivity and the absence of pre-adapted lacustrine species in the Neotropical realm (Fernando and Holcik, 1991; Gomes and Miranda, 2001). Moreover, the bathypelagic strata have abiotic limitations for fish, especially due to low dissolved oxygen concentrations (Fernando and Holcik, 1991; Agostinho et al., 1999; Gido et al., 2002).

In large reservoirs, the differences among the zones along the longitudinal gradient, and between the littoral and those of the horizontal and vertical gradients are well documented, but these patterns are not well described for small reservoirs (Agostinho et al., 2007a; Okada et al., 2005; Affonso et al., 2016). Nowadays, Brazil has 436 operating small power plants ("Pequenas Centrais Hidrelétricas – PCHs"; generation of energy varying from one to 30 MW), 29 under construction and 117 already approved, which corresponds to 65% of energy generation (ANEEL, 2016). In addition, in Brazil, the "Agência Nacional de Energia Elétrica" (ANEEL) considers that the impacts caused by the construction of small power plants are minor (Nilton, 2009). However, there are no published studies evaluating possible gradients in small reservoirs, if the fish fauna differs along the possible gradients, nor if the impacts are higher than expected, or if there is a need to review the ongoing legislation. To worsen the situation, little is known about the fish species inhabiting these near-future impounded rivers, because some of them have not been studied yet (*sensu* the Linnaean shortfall; Brito, 2010).

Therefore, our objective was to evaluate the longitudinal, horizontal, and vertical gradients in the fish assemblage of a small reservoir, based on the zonation concept proposed by Thornton et al. (1990). Specifically, we evaluated variations in some assemblage attributes (species richness and evenness), and variations in the assemblage structure along these gradients. Considering that water level variations affects the reservoir dynamics, and it varies over time, depending on dam operation and rain, we analyzed all variations trough time.

2. Material and Methods

2.1. Study area

As a model for our generalizations, we used the Mourão I Dam, located in the Mourão River (tributary of the Ivaí River; upper Paraná River basin). The dam was concluded in 1964, its height is 19 m, and it generates 8.2 MW (Figure 1). The reservoir covers an area of 11.3 Km^2, contains 65 million m^3 of water, and the hydraulic retention time is 70 days (ANEEL, 2004). Despite its small size, the Mourão Reservoir is one of the largest of its category and provides multiple uses to locals, from energy production to recreation, as several other reservoirs all over Brazil (Cruz and Fabrizy, 1995).

The region where the reservoir is located has a subtropical climate, with strong tropical influence, without

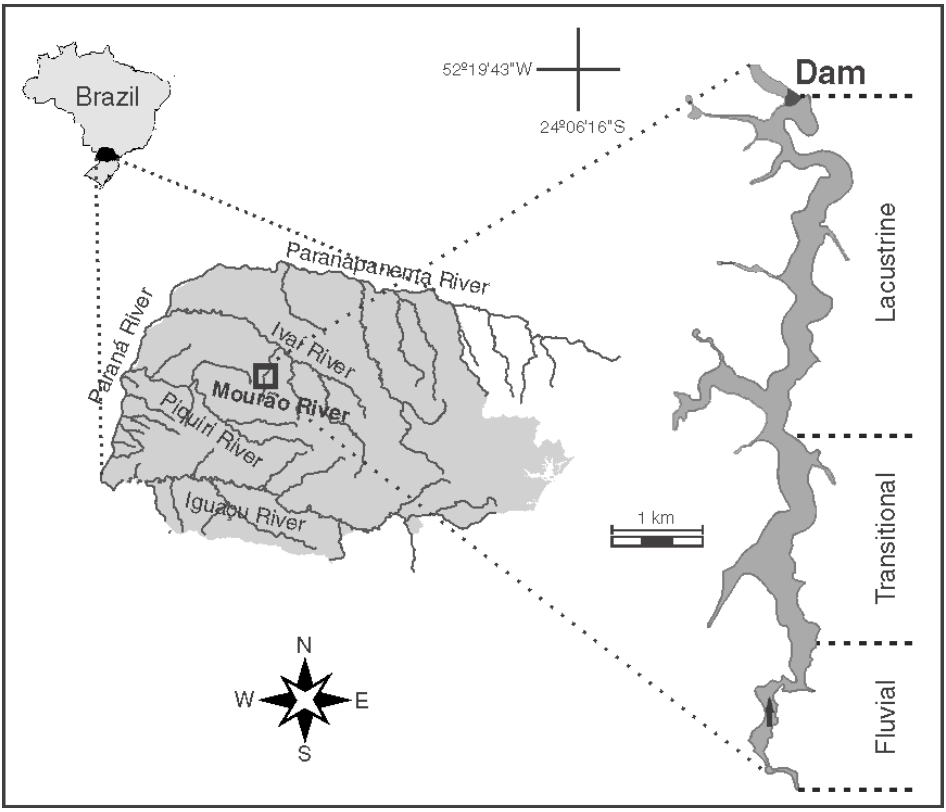

Figure 1. Map showing the location of Mourão Reservoir in the Paraná State and detail of shape and the longitudinal zonation.

well-defined seasonality. The land use in the areas adjacent to the reservoir is dominated by agriculture, precisely crops of soybeans. On its right margin (East), near the dam, is located the "Parque Estadual do Lago Azul", which represents a remnant of native secondary forest, but its left (West) side is occupied by a village for recreational purposes.

2.2. Sampling

Fish surveys were conducted by the "Companhia Paranaense de Energia" (COPEL), quarterly, from 2003 to 2008. To capture fish, 10 m long gillnets were used (mesh sizes: 2.4, 3, 4, 5, 6, 7, 8, 9, 10, 12, 14, and 16 cm; measured between opposite stretched knots) and trammel nets (inner mesh sizes: 6, 7, and 8 cm), set for 24 hours. Nets were arranged in three zones throughout the reservoir, following the concept of zonation proposed by Thornton et al. (1990) (fluvial, transitional, and lacustrine; longitudinal gradient; Figures 1 and 2). In each zone, the nets were set in three strata (littoral, pelagic, and bathypelagic; horizontal and vertical gradients; Figure 2). An entire set of nets was arranged in each stratum of each zone, and this sampling configuration allowed us to search for any existing spatial patterns.

Fishes were stored in 10% formalin and taken to the laboratories of the "Grupo de Pesquisas em Recursos Pesqueiros e Limnologia" (GERPEL), from the "Universidade Estadual do Oeste do Paraná" (UNIOESTE). Identification and taxonomic classification followed Graça and Pavanelli (2007), Langeani et al. (2007), and Garutti and Britski (2000).

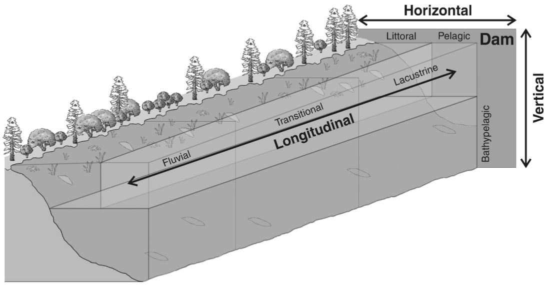

Figure 2. Diagram of the horizontal, vertical, and longitudinal gradients studied in the reservoir (Only illustrative; an entire set of gillnets was arranged in each stratum of each zone).

2.3. Data analysis

We considered our sample unit each set of nets in a given stratum, within each zone, at each month (totaling 198 samples - 3 zones * 3 strata * 4 months; unbalanced design; only three months sampled in 2003 and 2008). Data were expressed in a sample x species matrix, with the abundance of fish indexed by the catch per unit of effort (CPUE; number of individuals/1000 m^2 of gillnet in 24 h). Considering that water level variations affect the reservoir dynamics, and it varies over time depending on dam operation and rain, we analyzed all variations through time. Species richness and Shannon-Weiner evenness were calculated for each sample using the software PcOrd 6.0 (McCune and Mefford, 2011). Differences in these attributes, considering the factors zones (levels: fluvial, transitional, and lacustrine), strata (levels: littoral, pelagic, and bathypelagic), years (from 2003 to 2008), and their interactions were tested using three-way ANOVA (significance level: $p < 0.05$) in the software Statistica 7.1™ (Statsoft, 2005). When the ANOVA was significant, the post-hoc Tukey test was applied to identify which pair of levels of the factors (or the interactions) differed.

To summarize the structure of the fish assemblage, we applied a Correspondence Analysis (CA; McCune and Grace, 2002), using square root transformed data, and the option "*downweight rare species*" was selected, in the software PcOrd 6.0 (McCune and Mefford, 2011). We used CA because it better summarizes matrices with several zeroes and its orthogonal axes can be further used to hypothesis testing (Jackson et al., 2001). To test for significant differences in fish assemblage structure, according to the factors zones, strata, years, and their interactions, we applied a three-way ANOVA (and the post-hoc Tukey test, if necessary; in the software Statistica 7.1™) to the scores of the first two CA axes, retained for interpretation. To identify the most important species to the ordination, we correlated (Spearman rank correlation; in the software Statistica 7.1™) the CPUEs of each species in the square-rooted data matrix with each of the CA axes retained for interpretation.

3. Results

3.1. Variations in reservoir water level

Small reservoirs may present intense variations in water level, once they are usually located upper in watersheds, being very sensitive to local rains and droughts. This appears to be the case of Mourão Reservoir, which showed variations in water levels as high as five meters among years, except in March 2008, when this difference reached more than seven meters (almost 38% of the dam height; Figure 3). These variations have the potential to influence all biotic assemblages, including fish.

3.2. Ichthyofaunal survey

Samplings carried out in the Mourão Reservoir totaled 30,358 individuals belonging to six orders, 14 families, and 35 species (Table 1). Characidae (nine species) was the richest family, followed by Cichlidae (seven species). Catches were widely dominated by *Astyanax lacustris* and *Oligosarcus paranensis*, both Characidae, accounting for 61.8% and 25.4% of the total CPUE, respectively. The other species together accounted for only 12.8%. Overall, the littoral strata had higher abundances, although closely followed by the pelagic, especially at the beginning of the study. The bathypelagic, however, always presented the lower abundances, whatever the zone. The lacustrine zone presented the lowest general abundance (Figure 4). Considering the years, the highest total abundances were observed in 2003 (pelagic) and 2004 (littoral and pelagic), but with a clear decreasing trend over the years in the pelagic strata, in all zones.

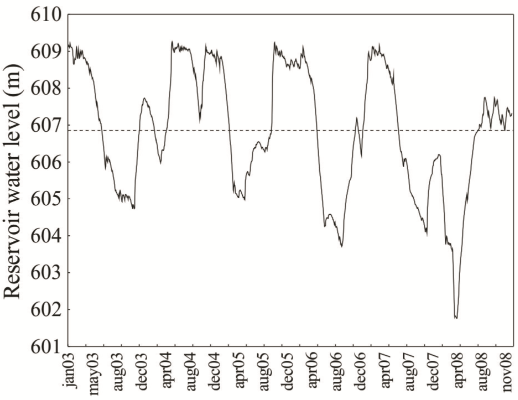

Figure 3. Water level of Mourão Reservoir from 2003 to 2008, dashed line represents the mean water level for this period. Source: UHE Mourão I Headquarters.

3.3. Spatial and temporal variations in assemblage attributes

The interaction between the factors zone and strata was significant for species richness ($F_{4;134} = 5.27$; $p < 0.01$), indicating different responses of the levels of one factor, considering the levels of the other (Figure 5). The littoral presented the higher averages of species richness, with higher values in the transitional zone (Tukey test in the interaction; $p < 0.05$). However, for the pelagic stratum, the fluvial zone presented higher averages (Tukey test in the interaction; $p < 0.05$), and no clear pattern was found for the bathypelagic stratum (Figure 5).

Overall evenness was considerably low (averages always below 0.65) showing elevated dominance in all samples (Figure 6). In addition, this attribute was highly variable among all zones and strata, specifically in the bathypelagic stratum of the lacustrine zone. This high variability was identified by the ANOVA, once the three-order interaction (zone*strata*years) was significant ($F_{20;134} = 1.66$; $p = 0.04$), indicating that there was not a clear trend among the factors.

3.4. Spatial and temporal variations in fish assemblage structure

In the ordination resulted from the Correspondence Analysis (CA; eigenvalues: CA1 = 0.20; CA2 = 0.18; Figure 7) it was possible to identify some differences in fish assemblage structure, especially considering the strata, with a clear trend of separation of the samples collected in the littoral stratum (positive signs), always concentrated in the upper part of the panel. Another strong segregation was observed for the pelagic stratum (triangles), but not

Table 1. Catch per unit of effort (CPUE; number of individuals/1000 m^2 in 24 hours) of collected fish and their taxonomic classification (according to Graça and Pavanelli, 2007; Langeani et al., 2007; Garutti and Britski, 2000), by zone (Fluvial, Transitional, and Lacustrine), and stratum (Litt: littoral, Pelag: pelagic, and Bathy: bathypelagic).

Zone:	**Fluvial**			**Transitional**			**Lacustrine**		
Stratum:	**Litt**	**Pelag**	**Bathy**	**Litt**	**Pelag**	**Bathy**	**Litt**	**Pelag**	**Bathy**
Characiformes									
Anostomidae									
Megaleporinus elongatus (Valenciennes, 1850)	0.50	0.88							
Megaleporinus macrocephalus (Garavello and Britski, 1988)	0.88								0.88
Characidae									
Astyanax aff. *bockmanni* Vari and Castro, 2007		0.50		2.63					
Astyanax aff. *fasciatus* (Cuvier, 1829)		2.63		7.00	0.88			0.88	
Astyanax aff. *paranae* Eigenmann, 1914	96.06	80.54	3.25	47.64	26.74	0.88	7.37	11.88	2.25
Astyanax lacustris (Lütken, 1875)	2072.28	2313.59	472.47	1976.54	2132.47	343.22	2876.78	1660.48	146.47
Astyanax sp. A		0.88		1.75	0.88				
Astyanax sp. B		0.50							
Oligosarcus paranensis Menezes and Géry, 1983	311.99	1145.20	829.33	311.46	1467.98	613.03	302.43	696.57	74.67
Oligosarcus pintoi Campos, 1945	0.88								
Salminus brasiliensis (Cuvier, 1816)		0.88		0.88					
Erythrinidae									
Hoplias lacerdae Miranda Ribeiro, 1908	3.13	1.37	1.50	1.87			2.75		
Hoplias sp. 1	16.64	6.13	0.88	19.01		0.88	11.38		
Hoplias sp. 2	78.91	18.39	11.38	43.64	2.25	4.00	44.02	0.88	0.88
Hoplias sp. 3	10.00		1.87	7.50			5.75		
Prochilodontidae									
Prochilodus lineatus (Valenciennes, 1836)	3.25	15.11	20.74	5.50	2.37		19.26	13.63	0.88
Cypriniformes									
Cyprinidae									
Cyprinus carpio Linnaeus, 1758	2.63	3.25	1.00	2.25	1.37				1.75
Gymnotiformes									
Gymnotidae									
‘	8.76			3.50	1.75	1.37	6.13		0.88
Gymnotus sylvius Albert and Fernandes-Matioli, 1999	3.62	1.00	3.49	2.37		1.00	0.50		

Table 1. Continued...

Zone:	Fluvial			Transitional			Lacustrine		
Stratum:	**Litt**	**Pelag**	**Bathy**	**Litt**	**Pelag**	**Bathy**	**Litt**	**Pelag**	**Bathy**
Perciformes									
Centrarchidae									
‘	1.75	1.37	1.37	4.00		0.88	8.76	0.50	0.88
Cichlidae									
Coptodon rendalli (Boulenger, 1897)	27.26	2.37	0.88	26.63			21.38		
Crenicichla britskii Kullander, 1982	17.50	0.88	4.49	27.01		4.00	29.14		2.25
Crenicichla haroldoi Luengo and Britski, 1974			0.88	4.38			2.63		
Crenicichla niederleinii (Holmberg, 1891)				0.88		0.88	2.00		
Cichlasoma paranaense Kullander, 1983	0.88						0.88		
Geophagus brasiliensis Quoy and Gaimard, 1824	205.06	25.01	17.25	368.43	0.88	19.26	324.68	2.87	8.38
Oreochromis niloticus (Linnaeus, 1758)	4.88	2.25	1.75	6.13			4.00	0.88	
Sciaenidae									
Plagioscion squamosissimus (Heckel, 1840)	21.01	134.84	165.11	39.40	95.44	55.16	75.30	43.78	3.50
Siluriformes									
Callichthyidae									
Callichthys callichthys (Linnaeus, 1758)							0.88		
Hoplosternum littorale (Hancock, 1828)		0.88							
Hepapteridae									
Rhamdia quelen (Quoy and Gaimard, 1824)	25.38	10.63	40.26	25.26	3.50	21.88	25.76	1.75	13.25
Loricariidae									
Hypostomus ancistroides (Ihering, 1911)		0.88							
Hypostomus aff. *commersoni* Valenciennes, 1836	18.38	19.99	29.75	14.88	5.00	19.63	37.51	2.75	3.75
Pimelodidae									
Pimelodus maculatus Lacépede, 1803							0.88		
Synbranchiformes									
Synbranchidae									
Synbranchus marmoratus Bloch, 1795	1.75	0.50		1.37		0.88			

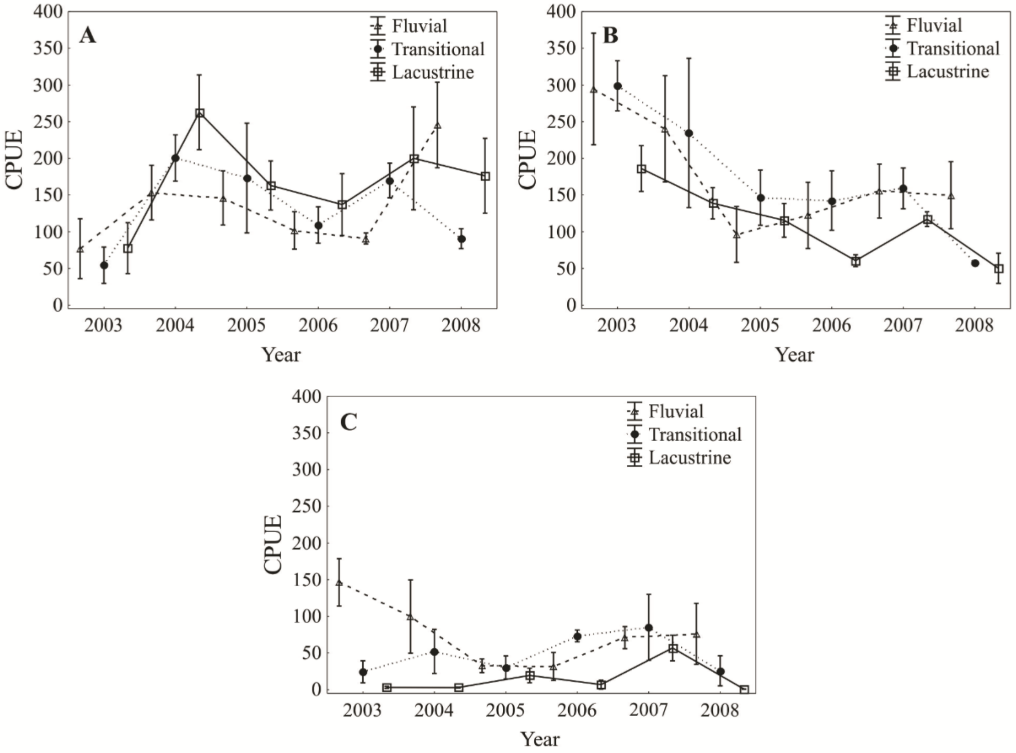

Figure 4. Mean (±standard error) of total abundance indexed by the capture per unit effort (CPUE; number of individuals/1000 m^2 of gillnet in 24 h) from 2003 to 2008, for all zones (fluvial, transitional, and lacustrine) in all three strata ((A) littoral; (B) pelagic; (C) bathypelagic), for the samples collected in the Mourão Reservoir.

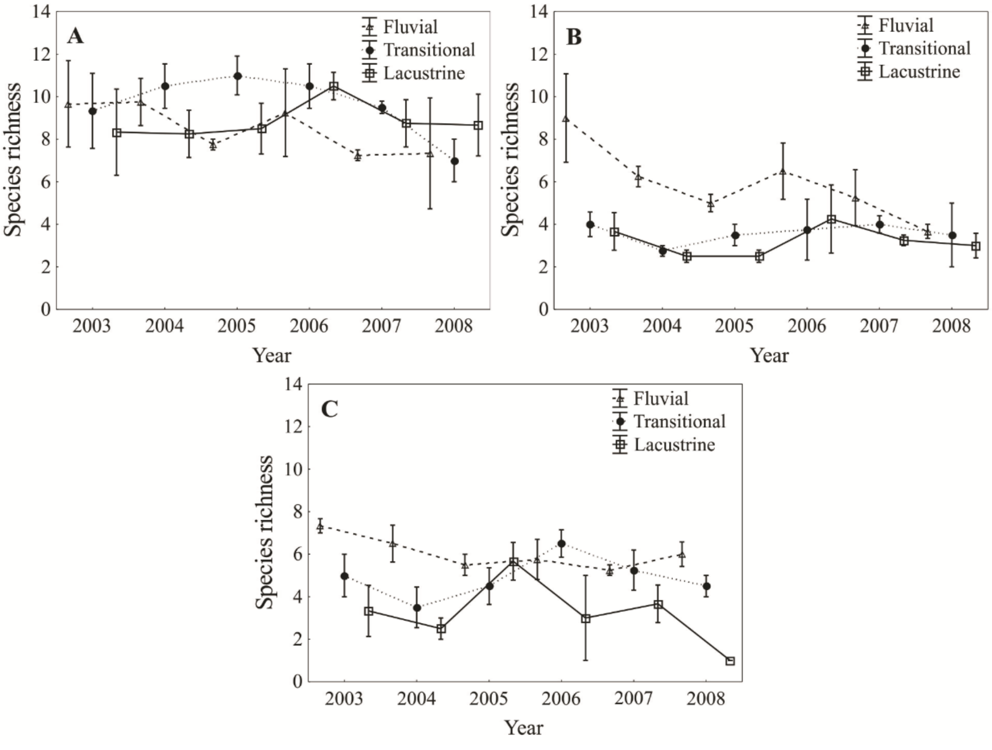

Figure 5. Mean (±standard error) of species richness (S) from 2003 to 2008, for all zones (fluvial, transitional, and lacustrine) in all three strata ((A) littoral; (B) pelagic; (C) bathypelagic), for the samples collected in the Mourão Reservoir.

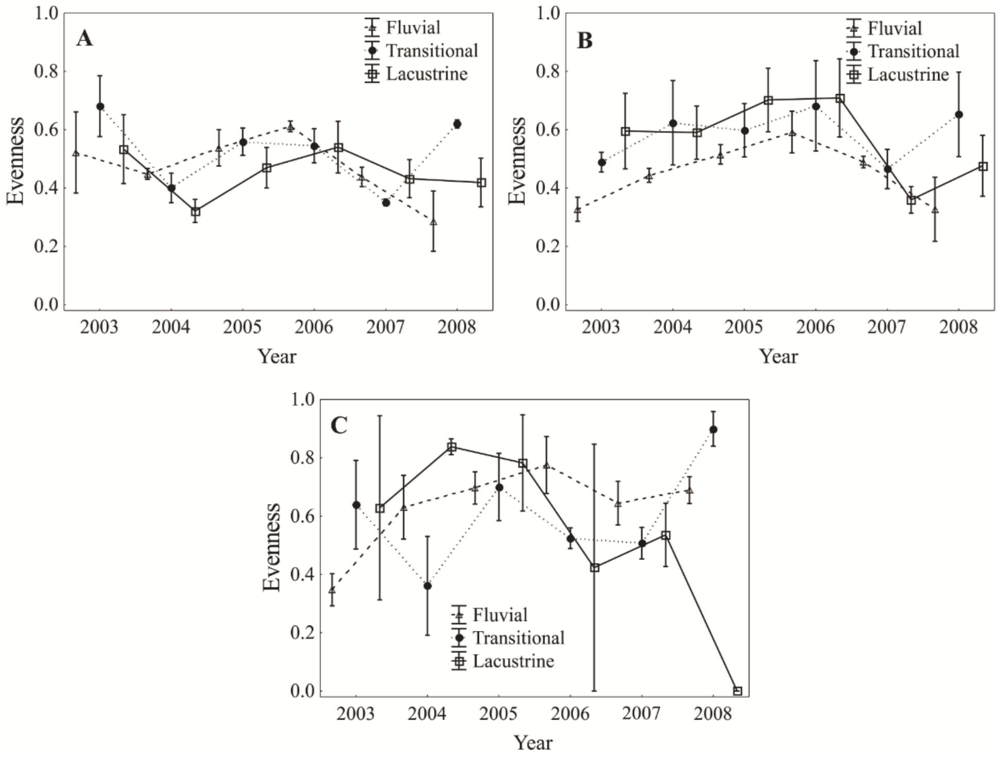

Figure 6. Mean (±standard error) of evenness (E) from 2003 to 2008, for all zones (fluvial, transitional, and lacustrine) in all three strata ((A) littoral; (B) pelagic; (C) bathypelagic), for the samples collected in the Mourão Reservoir.

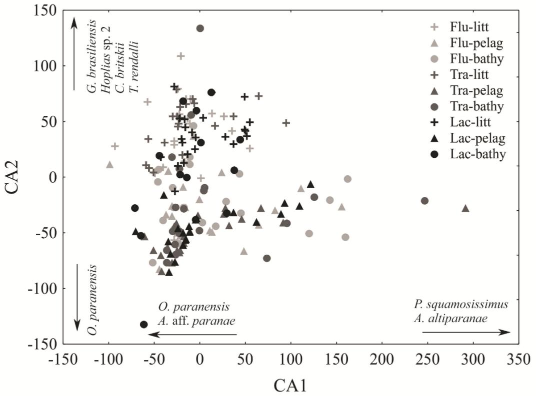

Figure 7. Correspondence Analysis (CA) on CPUE standardized square root transformed data for all species, separated by zones (light gray: fluvial; dark gray: transitional; black: lacustrine), and strata (cross: littoral; triangle: pelagic; circle: bathypelagic), for the samples collected in the Mourão Reservoir.

for the bathypelagic (circles). The same pattern was not clear for the zones.

The three-way ANOVA applied to CA1 revealed no significance for any interaction, which allowed interpreting the main factors. Thus, CA1 presented variations among strata ($F_{2;134} = 3.85$; $p = 0.02$) with the littoral differing from the bathypelagic (Tukey test; $p = 0.02$; Figure 6), and among years ($F_{2;134} = 45.12$; $p < 0.01$), with the years of 2007 and 2008 differing from all the others (Tukey test; $p < 0.01$; Figure 8).

For the CA2, the three-way ANOVA was significant for the interaction between zones and strata ($F_{4,134} = 3.26$; $p = 0.01$). Vertically, in the fluvial and transitional zones, the littoral had significantly higher scores than the others strata, and in the lacustrine zone, all strata were significantly different (Tukey test in the interaction; $p < 0.01$) (Figure 9).

Species that most explained the possible patterns were, for CA1, *Plagioscion squamosissimus* (ρ = 0.79) and *Astyanax lacustris* (ρ = 0.18), positively correlated, and *Oligosarcus paranensis* (ρ = -0.46) and *Astyanax* aff. *paranae* (ρ = -0.55), negatively correlated. These species presented high variability in abundance among zones and strata, but the species positively correlated (*P. squamosissimus*) presented increased abundance at the end of the study (Figure 10), whereas de negatively correlated (*O. paranensis*) presented the opposite trend (Figure 11). For CA2, species positively correlated were *Geophagus brasiliensis* (ρ = 0.71; Figure 12), *Hoplias* sp. 2 (ρ = 0.62), *Crenicichla britskii* (ρ = 0.58), and *Tilapia rendalli* (ρ = 0.53). Only *Oligosarcus paranensis* (ρ = -0.58) was negatively correlated to this axis. Overall, species positively correlated, presented high abundances only in the littoral stratum, whereas the negatively correlated had high abundances only in the pelagic stratum.

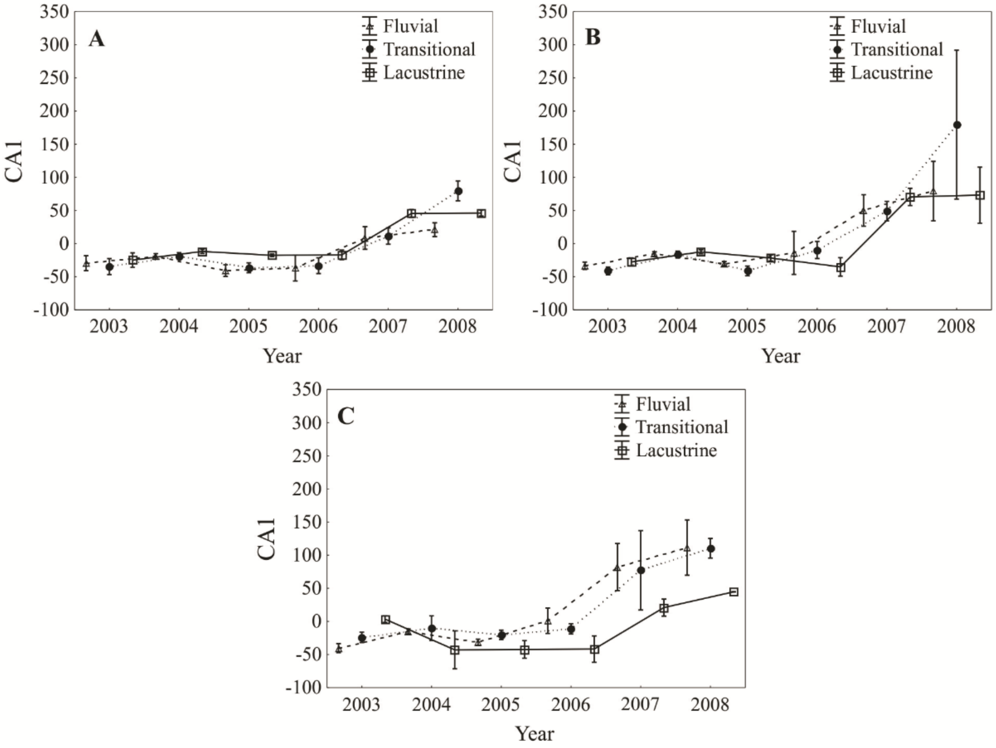

Figure 8. Mean (±standard error) of CA1 scores from 2003 to 2008, for all zones (fluvial, transitional, and lacustrine) in all three strata (A) littoral; (B) pelagic; (C) bathypelagic), for the samples collected in the Mourão Reservoir.

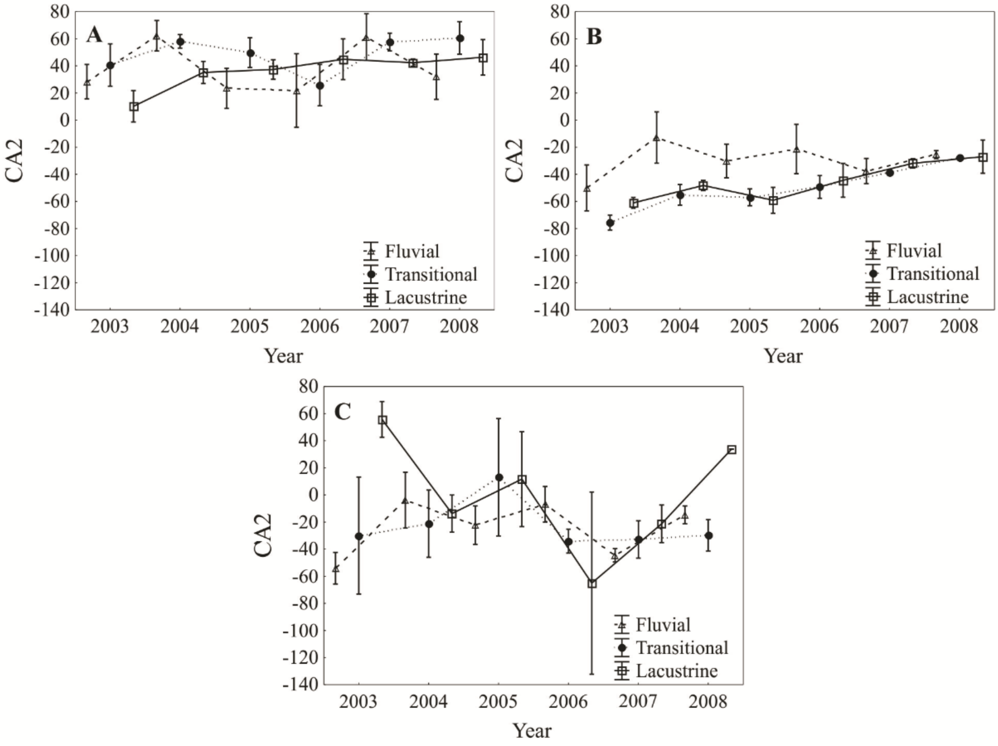

Figure 9. Mean (±standard error) of CA2 scores from 2003 to 2008, for all zones (fluvial, transitional, and lacustrine) in all three strata ((A) littoral; (B) pelagic; (C) bathypelagic), for the samples collected in the Mourão Reservoir.

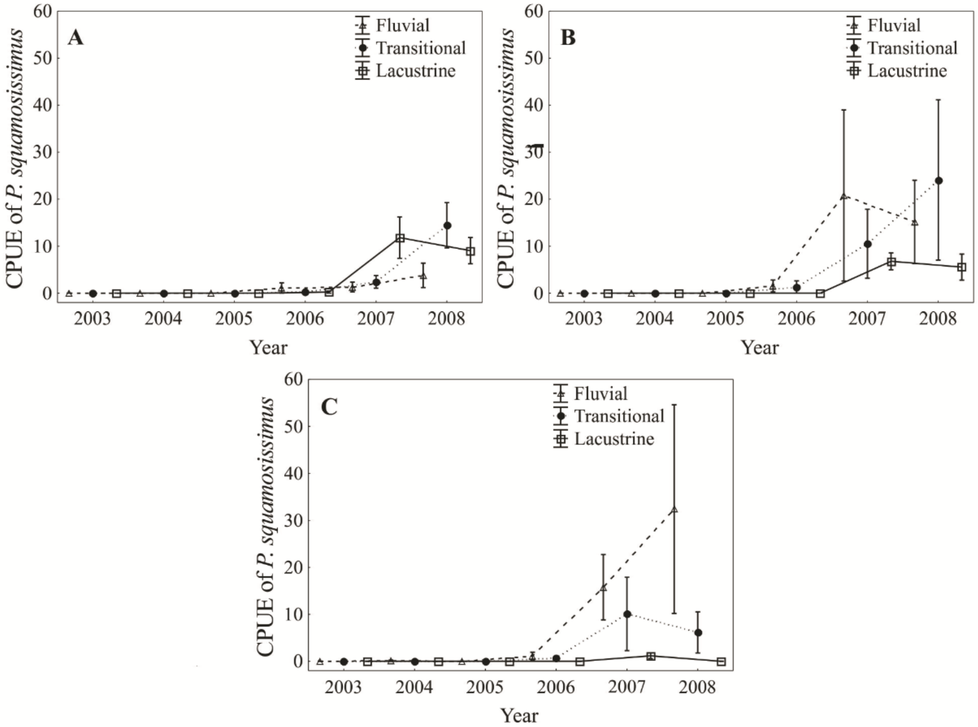

Figure 10. Mean (±standard error) of the abundance of *Plagioscion squamosissimus* (positively correlated with CA1), indexed by the CPUE (number of individuals/1000 m^2 of gillnet in 24 h), from 2003 to 2008, for all zones (fluvial, transitional, and lacustrine), and strata ((A) littoral; (B) pelagic; (C) bathypelagic), for the samples collected in the Mourão Reservoir.

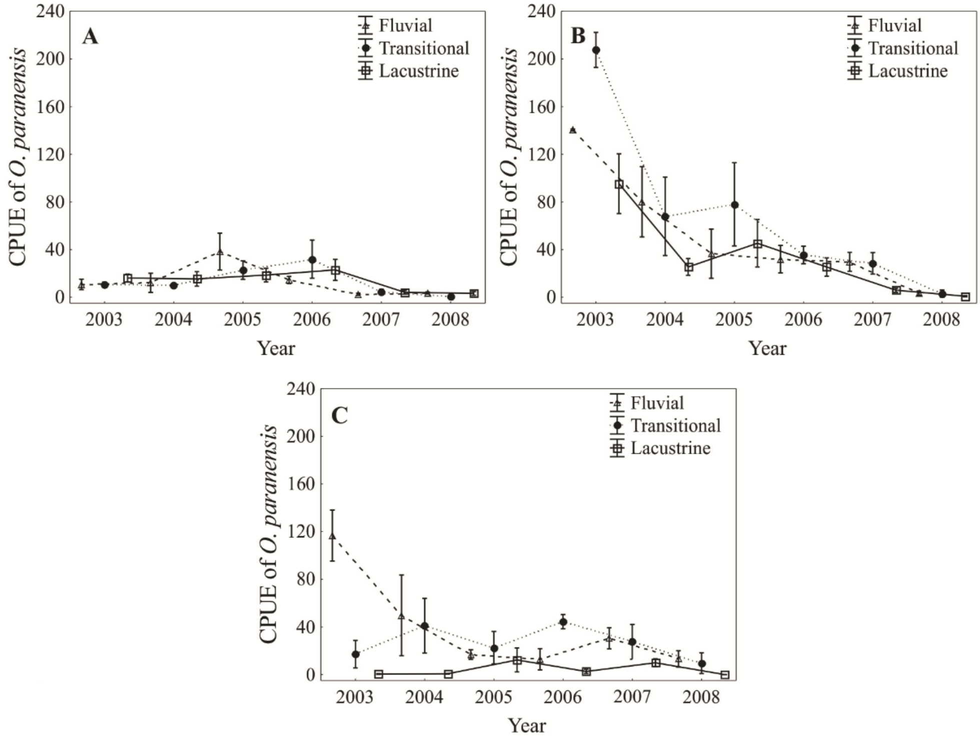

Figure 11. Mean (±standard error) of the abundance of *Oligosarcus paranensis* (negatively correlated with CA1), indexed by the CPUE (number of individuals/1000 m^2 of gillnet in 24 h), from 2003 to 2008, for all zones (fluvial, transitional, and lacustrine), and strata ((A) littoral; (B) pelagic; (C) bathypelagic), for the samples collected in the Mourão Reservoir.

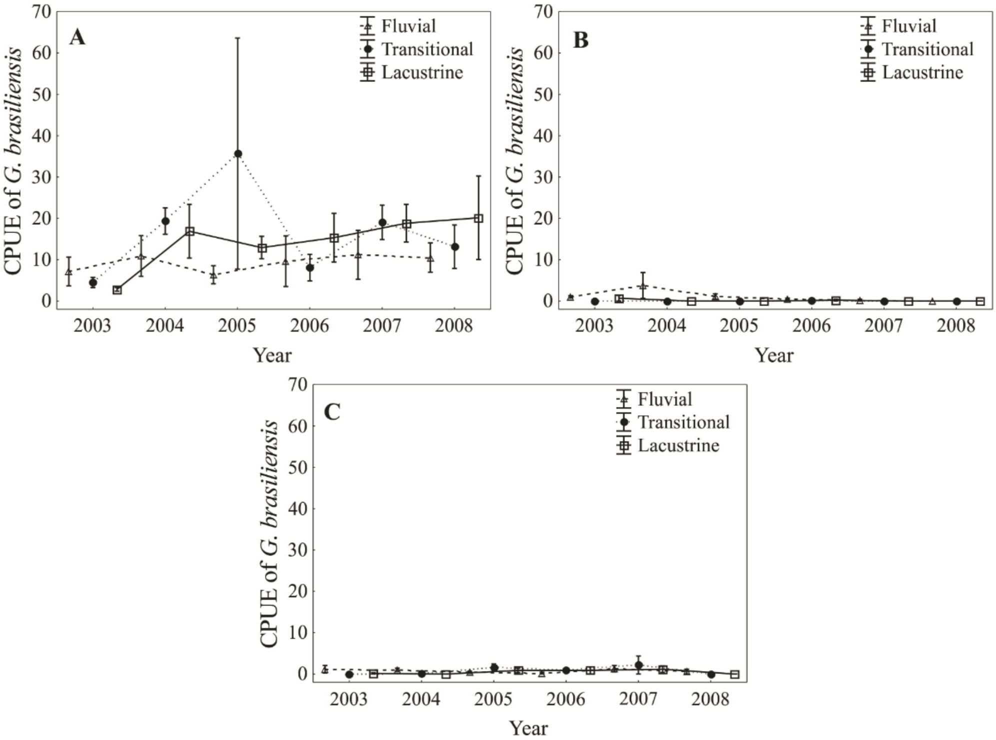

Figure 12. Mean (±standard error) of the abundance of *Geophagus brasiliensis* (positively correlated with CA2), indexed by the CPUE (number of individuals/1000 m^2 of gillnet in 24 h), from 2003 to 2008, for all zones (fluvial, transitional, and lacustrine), and strata ((A) littoral; (B) pelagic; (C) bathypelagic), for the samples collected in the Mourão Reservoir.

4. Discussion

Species richness presented the expected longitudinal gradient, decreasing from the fluvial to the lacustrine zone, in the pelagic and the bathypelagic strata. These longitudinal differences are consistent with the zonation concept proposed by Thornton et al. (1990), as already documented for fish assemblages in large reservoirs (Agostinho et al., 1999; Oliveira et al., 2004; Okada et al., 2005). Thus, our results indicate that even in small reservoirs, the upper reaches are capable of sustaining higher richness of riverine fish species, probably due to their similarity with natural habitats (Fernando and Holcik, 1991).

Considering the strata, the littoral presented the highest species richness in all zones, showing that fish prefer this region, similar to that observed in natural lakes (Gido and Matthews, 2000). This preference is probably related to the similarity between reservoir littoral regions and natural rivers in terms of habitat structure (Fernando and Holcik, 1991), and may sustain higher abundances of native fish (Gido et al., 2002). One factor that increases the species richness in the structured littoral stratum is that these environments provide natural nurseries for several fish species with parental care or species that lay their eggs on submerged structures, especially when the reservoir water level is high (Vazzoler and Menezes, 1992; Agostinho et al., 1999). Among the littoral strata, we suggest that the highest species richness found in the transitional zone is likely to be explained by the fact that this reservoir is small (short; slightly over 15 Km long), but has large lateral ponds that may occasionally supply resources to the reservoir, after a certain water level that connects them. These transient habitats would be responsible for nutrient input in the transitional zone, where water is calm, concentrating nutrients from the fluvial zone, as observed in large reservoirs, providing better conditions for the establishment of planktonic communities, attracting fish (Nogueira et al., 2006).

The expected longitudinal gradient in fish assemblage structure was not found in the littoral and the pelagic strata. We suggest that, despite the real differences observed in community attributes, they might not be able to distinguish three spatially distinct groups of fish in small reservoirs, in opposition to explicit patterns documented for large and cascade of reservoirs (Agostinho et al., 2004, 2007a; Gubiani et al., 2010). This longitudinal uniformity may be assigned also to the reservoir short length, and casual differences in fish assemblage structure among zones might be stochastic or due to particular interactions at some sites, decreasing the predictability of fish assemblage structure (Matthews et al., 2004). The apparent exception to this longitudinal homogeneity was the bathypelagic stratum of the lacustrine zone. This difference is possibly due to the strong lacustrine characteristics of this zone, with lower flow and greater depth (Thornton et al., 1990), which usually presents thermal stratification and low oxygen content (Esteves, 1998; Fernando and Holcik, 1991; Gido and Matthews, 2000; Edds et al., 2002).

Fish assemblage composition and structure presented the expected horizontal and vertical gradients, distinguishing all strata within each zone. These gradients were already documented for large reservoirs (Agostinho et al., 1999, 2007a; Vasek et al., 2009) and we suggest that such differences in spatial distribution results from horizontal and vertical abiotic and biotic gradients (Matthews et al., 2004). Horizontal differences in fish assemblage between the littoral and the pelagic strata are possibly because littoral stratum has features that can carry larger fish populations, such as in natural lakes and rivers (Fernando and Holcik, 1991; Edds et al., 2002). On the other hand, fishes are less abundant in the pelagic stratum and usually grouped in small shoals (Matthews et al., 2004). In the vertical gradient, we suggest that the association between oxygen and temperature provides adverse conditions for most fish species in deeper waters (Gido and Matthews, 2000).

The Mourão Reservoir fish assemblage was composed of a few species and largely dominated by *Astyanax lacustris* and *Oligosarcus paranensis* that, along with *Plagioscion squamosissimus*, seemed to drive the major differences in the observed patterns. *A. lacustris* is a small-bodied fish, with high fecundity, rapid development, and reach sexual maturity in a few months (Agostinho et al., 1999; Suzuki et al., 2005), which makes this species a great colonizer, as observed in several young reservoirs (Agostinho et al., 1999). In addition, this species has a wide feeding spectrum, ingesting algae, superior plants, several invertebrates, microcrustaceans, and detritus (Peretti and Andrian, 2008), despite being able to alternate among the items according to the availability. For these reasons, this species is able to sustain large populations, even if it faces periods of resource shortages. Also, as it promptly responds to the availability of resources, the fact that the reservoir presented substantial variations in water level every year (see Figure 3 for details), it may have incorporated feeding resources to the reservoir (similar to a drawdown), which would favor this opportunistic species, maintaining higher abundances along the study period.

On the other hand, *O. paranensis* is also documented as one of the fish species that succeeds in the occupation of reservoirs (Agostinho et al., 1999; Smith and Petrere Júnior, 2008), probably because of its fast growth, which means a rapid development (Abelha et al., 2012). In addition, the diet of this species is based mostly on invertebrates for juveniles and fish for adults, using natural habitat structures for predation (Casatti et al., 2001). Furthermore, despite the reservoir age and the advanced decomposition stages of trunks and branches, some remaining areas with submerged refuges are available, which are important habitat structures for fish hiding and escaping (Gois et al., 2012). Lastly, *P. squamosissimus*, also important in our study, is an introduced species from the Amazon basin, and the literature reports its success in reservoirs (Agostinho et al., 1994). This success can be addressed to its life-strategy features, especially those related to reproduction, once it is one of the few species with pre-adaptations to thrive in lentic (pelagic regions) systems (Gomes and Miranda, 2001), in addition to its feeding plasticity (Carnelós and Benedito-Cecílio, 2002). The inverse trends in the abundances of *O. paranensis* and *P. squamosissimus* suggest one being replaced by the other, probably because the second has more competitive advantages in the lentic waters of the reservoir.

The construction of dams in rivers for power generation is a fairly common practice in regions with a large number of rivers and rugged terrains. In this study, we observed that the Mourão Reservoir (a small reservoir) presented the same strong vertical and horizontal gradients identified in large reservoirs. The main difference was that small reservoirs did not present the expected strong longitudinal gradient in fish assemblage structure, as observed in the large ones. In addition, we observed high variation in fish assemblage structure through time, and this appears to be related to the variations in reservoir water level. This should be a concern to managers, especially because small alterations in reservoir water level should affect the entire system in a more severe way that occurs in large reservoirs. Therefore, our naïve belief that small reservoirs cause fewer impacts than large ones appears now clearly dismissed, and we were actually underestimating the environmental effects of small power plants. Remember, this study just considered the reservoir area, not the downstream effects. Finally, we hope that the generalizations made in this study may apply to several small reservoirs in the Neotropical region and elsewhere. We also believe that this study is a start point for studies that gather information from several small reservoirs, seeking broader patterns that can apply to several other similar environments in a broader spatial scale, including pre and post impoundment studies for a better evaluation of the impacts of these dams.

5. Conclusion

The expected longitudinal and horizontal gradients were found for the attributes and structure of the fish assemblage of the Mourão reservoir. The longitudinal gradient, evident in large reservoirs, was not observed for this small reservoir. Thus, our results imply that, although smaller in water volume and especially in length, related to large reservoirs, spatiality is a structuring agent of the fish assemblage of small reservoirs, favoring species that occupies the littoral stratum, in all zones, especially in riverine and transitional zones.

Therefore, we conclude that the potential impacts of building small dams, on fish, are comparable to those of large reservoirs, in terms of spatial changes, which are detrimental to species persistence. More importantly, legislation concerning such aspects as construction and especially the environmental assessment seriousness should be urgently and carefully reviewed. Furthermore, this study contributes with information on the spatial organization of fish assemblages in small reservoirs, in search of broader patterns.

Acknowledgments

We thank to the Companhia Paranaense de Energia Elétrica (COPEL) and the Grupo de Pesquisas em Recursos pesqueiros e Limnologia (GERPEL) for data collection and laboratory analysis.

References

ABELHA, M.C.F., KASHIWAQUI, E.A.L. and GOULART, E., 2012. Population structure, condition and diet of *Oligosarcus paranensis* (Menezes & Gery, 1983) (Osteichthyes: Characidae) at two reservoirs in South Brazil. *Biota Neotropica*, vol. 12, no. 1, pp. 187-197. http://dx.doi.org/10.1590/S1676-06032012000100015.

AFFONSO, I.P., GOMES, L.C., AGOSTINHO, A.A., MESSAGE, H.J., LATINI, J.D. and GARCÍA-BERTHOU, E., 2016. Interacting effects of spatial gradients and fishing gears on characterization of fish assemblages in large reservoirs. *Reviews in Fish Biology and Fisheries*, vol. 26, no. 1, pp. 71-81. http://dx.doi.org/10.1007/s11160-015-9402-1.

AGÊNCIA NACIONAL DE ENERGIA ELÉTRICA – ANEEL, 2004. *Resolução normativa nº 91, de 10 de fevereiro de 2004*. Diário Oficial da República Federativa do Brasil, Brasília, 10 fev.

AGÊNCIA NACIONAL DE ENERGIA ELÉTRICA – ANEEL, 2016. *Banco de Informações de Geração – BIG*. Brasília: ANEEL.

AGOSTINHO, A. A., JÚLIO JÚNIOR, H. F. and PETRERE JÚNIOR, M., 1994. Itaipu reservoir (Brazil): impacts of the impoundment on the fish fauna and fisheries. In: I.G. COWX, ed. *Rehabilitation of freshwater fisheries*. Osney Mead: Fishing News Books, pp. 171-184.

AGOSTINHO, A.A., MIRANDA, L.E., BINI, L.M., GOMES, L.C., THOMAZ, S.M. and SUZUKI, H.I., 1999. Patterns of colonization in Neotropical reservoirs, and prognoses on aging. In: J.G. TUNDISI and M. STRASKRABA, eds. *Theoretical reservoir ecology and its applications*. São Carlos: International Institute of Ecology, pp. 227-265.

AGOSTINHO, A.A., GOMES, L.C., VERÍSSIMO, S. and OKADA, E.K., 2004. Flood regime, dam regulation and fish in the Upper Paraná River: effects on assemblage attributes, reproduction and recruitment. *Reviews in Fish Biology and Fisheries*, vol. 14, no. 1, pp. 11-19. http://dx.doi.org/10.1007/s11160-004-3551-y.

AGOSTINHO, A.A., GOMES, L.C. and PELICICE, F.M., 2007a. *Ecologia e manejo de recursos pesqueiros em reservatórios do Brasil*. Maringá: Eduem. 501 p.

AGOSTINHO, A.A., PELICICE, F.M., PETRY, A.C., GOMES, L.C. and JÚLIO JÚNIOR, H.F., 2007b. Fish diversity in the upper Paraná River basin: habitats, fisheries, management and conservation. *Aquatic Ecosystem Health & Management*, vol. 10, no. 2, pp. 174-186. http://dx.doi.org/10.1080/14634980701341719.

AGOSTINHO, A.A., PELICICE, F.M. and GOMES, L.C., 2008. Dams and the fish fauna of the Neotropical region: impacts and management related to diversity and fisheries. *Brazilian Journal of Biology = Revista Brasileira de Biologia*, vol. 68, no. 4, suppl., pp. 1119-1132. PMid:19197482. http://dx.doi.org/10.1590/S1519-69842008000500019.

AGOSTINHO, A.A., GOMES, L.C., SANTOS, N.C.L., ORTEGA, J.C.G. and PELICICE, F.M., 2016. Fish assemblages in Neotropical reservoirs: Colonization patterns, impacts and management. *Fisheries Research*, vol. 173, pp. 26-36. http://dx.doi.org/10.1016/j.fishres.2015.04.006.

BAUMGARTNER, G., NAKATANI, K., GOMES, L.C., BIALETZKI, A., SANCHES, P.V. and MAKRAKIS, M.C., 2008. Fish larvae from the upper Paraná River: Do abiotic factors affect larval density? *Neotropical Ichthyology*, vol. 6, no. 4, pp. 551-558. http://dx.doi.org/10.1590/S1679-62252008000400002.

BRITO, D., 2010. Overcoming the Linnean shortfall: data deficiency and biological survey priorities. *Basic and Applied Ecology*, vol. 11, no. 8, pp. 709-713. http://dx.doi.org/10.1016/j.baae.2010.09.007.

CARNELÓS, R.C. and BENEDITO-CECÍLIO, E., 2002. Reproductive Strategies of *Plagioscion squamosissimus* Heckel, 1840 (Osteichthyes Sciaenidae) in the Itaipu Reservoir, Brazil. *Brazilian Archives of Biology and Technology*, vol. 45, no. 3, pp. 317-324. http://dx.doi.org/10.1590/S1516-89132002000300010.

CASATTI, L., LANGEANI, F. and CASTRO, R.M.C., 2001. Peixes de riacho do Parque Estadual Morro do Diabo, bacia do Alto Rio Paraná, São Paulo. *Biota Neotropica*, vol. 1, no. 1, pp. 1-15. http://dx.doi.org/10.1590/S1676-06032001000100005.

CRUZ, H.C. and FABRIZY, N.L.P., 1995. Impactos ambientais de reservatórios e perspectivas de uso múltiplo. *Revista Brasileira de Energia*, vol. 4, no. 1, pp. 1-7.

EDDS, D.E., MATTHEWS, W.J. and GELWICK, F.P., 2002. Resource use by large catfishes in a reservoir: is there evidence for interactive segregation and innate differences? *Journal of Fish Biology*, vol. 60, no. 3, pp. 739-750. http://dx.doi.org/10.1111/j.1095-8649.2002.tb01698.x.

ESTEVES, F.A., 1998. *Fundamentos de Limnologia*. 2nd ed. Rio de Janeiro: Interciência. 602 p.

FERNANDO, C.H. and HOLCIK, J., 1991. Fish in reservoirs. *Internationale Revue der Gesamten Hydrobiologie und Hydrographie*, vol. 76, no. 2, pp. 149-167. http://dx.doi.org/10.1002/iroh.19910760202.

GARUTTI, V. and BRITSKI, H.A., 2000. Descrição de uma espécie nova de *Astyanax* (Teleostei: Characidae) da bacia do alto Rio Paraná e considerações sobre as demais espécies do gênero na bacia. *Comunicações do Museu de Ciências e Tecnologia da PUCRS. Série Zoologia*, vol. 13, pp. 64-88.

GIDO, K.B. and MATTHEWS, W.J., 2000. Dynamics of the offshore fish assemblage in a southwestern reservoir (Lake Texoma, Oklahoma, Texas). *Copeia*, vol. 2000, no. 4, pp. 917-930. http://dx.doi.org/10.1643/0045-8511(2000)000[0917:DOTOFA]2.0.CO;2.

GIDO, K.B., HARGRAVE, C.W., MATTHEWS, W.J., SCHNELL, G.D., POGUE, D.W. and SEWELL, G.W., 2002. Structure of littoral-zone fish communities in relation to habitat, physical, and chemical gradients in a southern reservoir. *Environmental Biology of Fishes*, vol. 63, no. 3, pp. 253-263. http://dx.doi.org/10.1023/A:1014359311188.

GIDO, K.B., SCHAEFER, J.F. and FALKE, J.A., 2009. Convergence of fish communities from the littoral zone of reservoirs. *Freshwater Biology*, vol. 54, no. 6, pp. 1163-1177. http://dx.doi.org/10.1111/j.1365-2427.2008.02162.x.

GOIS, K.S., ANTONIO, R.R., GOMES, L.C., PELICICE, F.M. and AGOSTINHO, A.A., 2012. The role of submerged trees in structuring fish assemblages in reservoirs: two case studies in South America. *Hydrobiologia*, vol. 685, no. 1, pp. 109-119. PMid:24683268. http://dx.doi.org/10.1007/s10750-011-0843-9.

GOMES, L.C. and MIRANDA, L.E., 2001. Riverine characteristics dictate composition of fish assemblages and limit fisheries in reservoirs of the upper Paraná River basin. *River Research and Applications*, vol. 17, no. 1, pp. 67-76.

GRAÇA, W.J. and PAVANELLI, C.S., 2007. *Peixes da planície de inundação do alto rio Paraná e áreas adjacentes*. Maringá: Eduem. 241 p.

GUBIANI, E.A., GOMES, L.C., AGOSTINHO, A.A. and BAUMGARTNER, G., 2010. Variations in fish assemblages in a tributary of the upper Paraná River, Brazil: a comparison between pre and post-closure phases of dams. *River Research and Applications*, vol. 26, no. 7, pp. 848-865. http://dx.doi.org/10.1002/rra.1298.

JACKSON, D.A., PERES-NETO, P.R. and OLDEN, J.D., 2001. What controls who is where in freshwater fish communities: the roles of biotic, abiotic, and spatial factors. *Canadian Journal of Fisheries and Aquatic Sciences*, vol. 58, no. 1, pp. 157-170.

KIMMEL, B.L., LIND, O.T. and PAULSON, J.L., 1990. Reservoir ecosystems: conclusions and speculations. In: K.W. THORNTON, B.L. KIMMEL and F.E. PAYNE, eds. *Reservoir limnology: ecological perspectives*. New York: John Wiley & Sons, pp. 133-194.

LANGEANI, F., CASTRO, R.M.C., OYAKAWA, O.T., SHIBATTA, O.A., PAVANELLI, C.S. and CASATTI, L., 2007. Diversidade da ictiofauna do Alto Rio Paraná: composição atual e perspectivas futuras. *Biota Neotropica*, vol. 7, no. 3, pp. 181-197. http://dx.doi.org/10.1590/S1676-06032007000300020.

MATTHEWS, W.J., GIDO, K.B. and GELWICK, F.P., 2004. Fish assemblages of reservoirs, illustrated by Lake Texoma (Oklahoma-Texas, USA) as a representative system. *Lake and Reservoir Management*, vol. 20, no. 3, pp. 219-239. http://dx.doi.org/10.1080/07438140409354246.

MCCUNE, B. and GRACE, J.B., 2002. *Analysis of ecological communities*. Oregon: MjM Software Design. 304 p.

MCCUNE, B. and MEFFORD, M.J., 2011. *PC-ORD multivariate analysis of ecological data. Version 6.18*. Oregon: MjM Software.

MIRANDA, L.E. and RABORN, S.W., 2000. From zonation to connectivity: fluvial ecology paradigms of the 20th century. *Polskie Archiwum Hydrobiologii*, vol. 47, no. 1, pp. 5-19.

NILTON, C.L., 2009. *O impacto das Pequenas Centrais Hidrelétricas (PCHs) no meio ambiente*. Lavras: Universidade Federal de Lavras, 17 p. Monografia de Especialização em Formas Alternativas de Energia.

NOBLE, R.L., 1980. Management of lakes, reservoirs and pounds. In: R.T. LACKLEY and L.A. NIELSEN, eds. *Fisheries management*. Oxford: Blackwell Scientific Publications, pp. 265-295.

NOGUEIRA, M.G., HENRI, R. and JORCIN, A., 2006. *Ecologia de reservatórios: impactos potenciais, ações de manejo e sistemas em cascata*. São Carlos: Rima. 472 p.

NOGUEIRA, M.G., PERBICHE-NEVES, G. and NALIATO, D., 2012. Limnology of two contrasting hydroelectric reservoirs (Storage and Run-of-River) in Southeast Brazil. In: H. SAMADI-BOROUJENI, ed. *Hydropower: practice and Application*. Rijeka: InTech, pp. 167-184.

OKADA, E.K., AGOSTINHO, A.A. and GOMES, L.C., 2005. Spatial and temporal gradients in artisanal fisheries of a large Neotropical reservoir in the Itaipu Reservoir, Brazil. *Canadian Journal of Fisheries and Aquatic Sciences*, vol. 62, no. 3, pp. 714-724. http://dx.doi.org/10.1139/f05-015.

OLIVEIRA, E.F., GOULART, E. and MINTE-VERA, C.V., 2004. Fish diversity along spatial gradients in the Itaipu reservoir, Paraná, Brazil. *Brazilian Journal of Biology = Revista Brasileira de Biologia*, vol. 64, no. 3A, pp. 447-458. PMid:15622842. http://dx.doi.org/10.1590/S1519-69842004000300008.

PERETTI, D. and ANDRIAN, I.F., 2008. Feeding and morphological analysis of the digestive tract of four species of fish (*Astyanax altiparanae, Parauchenipterus galeatus, Serrasalmus marginatus* and *Hoplias* aff. *malabaricus*) from the upper Paraná River floodplain, Brazil. *Brazilian Journal of Biology = Revista Brasileira de Biologia*, vol. 68, no. 3, pp. 671-679. PMid:18833491. http://dx.doi.org/10.1590/S1519-69842008000300027.

SMITH, W.S. and PETRERE JÚNIOR, J.R.M., 2008. Spatial and temporal patterns and their influence on fish community at Itupararanga Reservoir, Brazil. *Revista de Biología Tropical*, vol. 56, no. 4, pp. 2005-2020. PMid:19419097.

STATSOFT, 2005 [viewed 10 October 2016]. *STATISTICA (data analysis software system). Version 7.1* [software]. Available from: www.statistica.com

SUZUKI, H.I., BULLA, C.K., AGOSTINHO, A.A. and GOMES, L.C., 2005. Estratégias reprodutivas de assembleias de peixes em reservatórios. In: L. RODRIGUES, S.M. THOMAZ, A.A. AGOSTINHO and L.C. GOMES, eds. *Biocenoses em Reservatórios: padrões espaciais e temporais*. São Carlos: Rima, pp. 223-236.

THORNTON, K.W., KIMMEL, B.L. and PAYNE, F.E., 1990. *Reservoir limnology: ecological perspectives*. New Jersey: John Willey & Sons. 246 p.

TOLMASQUIM, M.T., 2012. The energy sector in Brazil: policy and perspectives. *Estudos Avançados*, vol. 26, no. 74, pp. 249-260.

VASEK, M., KUBECKA, J., CECH, M., DRAŠTÍK, V., MATĚNA, J., MRKVIČKA, T., PETERKA, J. and PRCHALOVÁ, M., 2009. Diel variation in gillnet catches and vertical distribution of pelagic fishes in a stratified European reservoir. *Fisheries Research*, vol. 96, no. 1, pp. 64-69. http://dx.doi.org/10.1016/j.fishres.2008.09.010.

VASEK, M., KUBECKA, J., PETERKA, J., ČECH, M., DRAŠTÍK, V., HLADÍK, M., PRCHALOVÁ, M. and FROUZOVÁ, J., 2004. Longitudinal and vertical spatial gradients in the distribution of fish within a Canyon-Shaped reservoir. *International Review of Hydrobiology*, vol. 89, no. 4, pp. 352-362. http://dx.doi.org/10.1002/iroh.200410734.

VAZZOLER, A.E.A.M. and MENEZES, N.A., 1992. Síntese de conhecimento sobre o comportamento reprodutivo dos Characiformes da América do Sul (Teleostei, Ostariophysi). *Brazilian Journal of Biology = Revista Brasileira de Biologia*, vol. 52, no. 4, pp. 627-640.